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Two new Central European subspecies of *Leptothorax nylanderi* (Förster, 1850) and *Leptothorax sordidulus* Müller, 1923 (Hymenoptera: Formicidae)

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Mit 20 Abbildungen und 8 Tabellen

Abstract

Two new taxa closely related to *Leptothorax nylanderi* (Förster, 1850) and *Leptothorax sordidulus* Müller, 1923 are described: *Leptothorax nylanderi slavonicus* n. ssp. and *Leptothorax sordidulus saxonicus* n. ssp. *L. nylanderi nylanderi* and *L. nylanderi slavonicus* are considered as distinct parapatric subspecies which have spread from different pleistocene refuge areas and have met in E Germany 7000-8000 BP. *Nylanderi* invaded Central Europe from the SW while *slavonicus* immigrated from the Balkans. They apparently hybridize in the contact zone but have maintained their morphological differences. *Leptothorax sordidulus saxonicus* and *L. sordidulus sordidulus* probably represent a similar phenomenon. *Sordidulus*, spreading from a refuge in the S Appennines, invaded N Italy, W Austria, Slovenia, Croatia and NW Serbia. *Saxonicus*, having a S Balkan refuge, spread to E Austria, Slovakia, Moravia, Bohemia and Saxony. *Sordidulus* and *saxonicus* are probably in contact in E Austria, Slovenia and NW Serbia. However, the situation in this contact zone remains to be studied. The relations to the taxa *L. melas* Espadaler, Plateaux & Casevitz-Weulersse, 1984, *carinthiacus* Bernard, 1957 and *normandi* Santschi, 1912 are discussed on the basis of type series. *L. carinthiacus* is very certainly a synonym of *sordidulus*.

1. Introduction

Electrophoretic investigations of allozymes performed by Per Douwes and his cooperators at the Lund University (DOUWES pers. communication) gave evidence that the Central European *Leptothorax nylanderi* can be split into two genetically distinct populations which are fixed for different alleles. My own investigations on the external morphology fully confirmed the presence of two distinct, parapatric populations. The western population, which has apparently spread from a SW European and/or S Italian refuge area after the end of the Younger Dryas period must be referred to

as the true *Leptothorax nylanderi* Förster (the types of *nylanderi* are lost, but Förster's type locality is a clear indication). The eastern population, which has most certainly spread from a S Balkan refuge, is described here as *Leptothorax nylanderi slavonicus* subspecies nova. Known front lines where the two parapatric taxa are presently in contact go through East Germany and North Italy.

Certain xerothermous spots of deciduous woodland situated on south-exposed rock slopes in the region of Saxony/East Germany are inhabited by a *Leptothorax* species that is by morphology and habitat selection clearly different from both *nylanderi* and *slavonicus*. In previous papers this species has been referred to as *Leptothorax sordidulus* Müller, 1923 (SEIFERT 1986) and *Leptothorax* aff. *sordidulus* sp. Sax (SEIFERT 1993, 1994). Meanwhile there is evidence that this ant is a taxon different from *sordidulus*. *L. sordidulus* has certainly spread from a Pleistocene refuge area in the S Appenines while *L. saxonicus* is most probably of a S Balkan origin. *L. saxonicus* is described here as a eastern subspecies of *sordidulus*. The situation in the contact zone of *sordidulus* and *saxonicus* in E Austria, Slovenia and NW Serbia is poorly studied but it seems that intermediates are very rare.

2. Terminology and methods of morphological investigation

All measurements were taken using the stereomicroscopes Technival (Carl Zeiss Jena) and Wild M10 (Leica) at a magnification of 80 – 320x. The maximum possible magnification to keep a structure within the range of the ocular micrometer was used. A mean measuring error of $\pm 1 \mu\text{m}$ is given for small and well-defined structures such as petiole width, but may reach 5 μm for large measures with difficult positioning and high dependency from air humidity. To avoid rounding errors, all measurements have been recorded in μm even for characters where a precision of $\pm 1 \mu\text{m}$ is impossible.

If not otherwise stated, statistic tests tested the equality of mean values: a *t* test was applied, when an *F* test proved the equality of the variances; otherwise a modified *t* test with corrected degrees of freedom according to WELCH (1947) was applied.

In order to reduce irritating reflexions of the cuticular surfaces and to get an improved visualization of the microsculpture, a plastic diffusor was positioned as close as possible to the specimen.

- FR width of frontal carinae immediately posterior of the scape insertion. (When the scape is directed strictly caudad, the inner corner of scape base is harboured in an excavation below the frontal carinae. The outlines of this excavation shine through the carinae and mark the measuring line for FR.)
- ISP propodeal spine index measured in lateral view: the distance from spine tip to the centre of the propodeal spiracle divided through the smallest distance between the centre of the spiracle and the margin of the infraspinal excavation.
- HL maximum head length in median line; the head must be carefully tilted to the position with real maximum
- HW maximum head width across eyes
- HS head 'size'; the arithmetic mean of HL and HW, used as a less variable indicator of body size.
- ML mesosoma length in the sexuals; measured in lateral view from the anteriormost point of the frontal face of pronotum to the posterior margin of the lateral propodeal lobe
- MW mesosoma width; that is, across the propodeum in the worker and immediately frontal of the tegulae in the sexuals.
- PE maximum petiole width
- PP maximum postpetiole width
- SL maximum straight line scape length excluding the articular condyle
- SPBA the smallest distance of the lateral margins of the spines at their base. This should be measured under conditions of transmitted-light and in dorsofrontal view, since the wider parts of the ventral propodeum do not interfere the measurement in this position.
- SPTI the maximum distance between the lateral margins of the propodeal spines. SPTI is often positioned near the spine tips but is found in a more proximal position in case of distally incurved spines. The ratio SPTI/SPBA is a measure of spine divergence.

3. Material studied

Of *L. n. slavonicus* a total of 1100 workers and 233 queens belonging to 275 samples was studied. 88% of this material came from East Germany and 12% from Bohemia, Austria, NE Italy, Slovenia, Bosnia, and Bulgaria.

Material of *L. nylanderi* (Förster, 1850) for comparison included about 1000 workers and 153 queens belonging to 215 samples (94% Germany, 6% North Italy and Sweden).

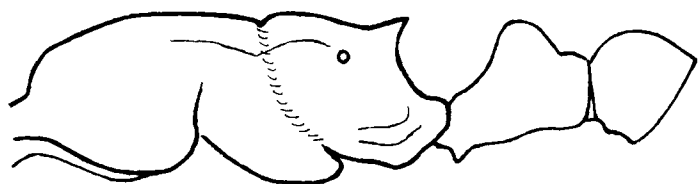


FIG. 1 SORD

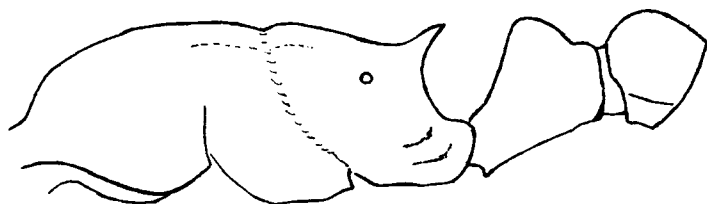


FIG. 2 SAXO

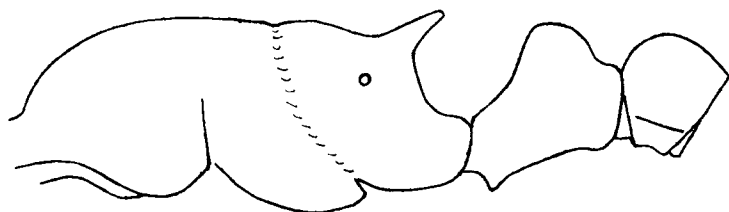


FIG. 3 NYLA



FIG. 5 NYLA

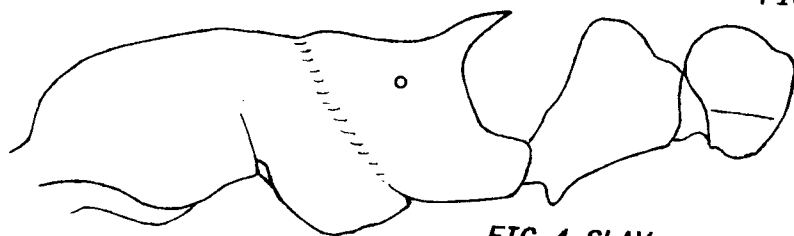


FIG. 4 SLAV



FIG. 6 SLAV

Figs. 1, 2, 3, 5 Mesosoma, petiole and postpetiole of worker of *Leptothorax s. sordidulus*, *s. saxonicus*, *n. nylander* and *n. slavonicus* in lateral view. Figs. 4, 6: Outlines of propodeal spines and propodeal spiracles of workers of *L. n. nylander* and *n. slavonicus* in dorsofrontal view. The scale bar represents 512 μ m

Of *L. sordidulus* Müller, 1923, 70 workers and 20 queens from 21 nest samples were studied. The material was collected in NE Italy, Austria, Slovenia, Croatia and N Serbia and included a type queen and 3 worker types of *L. carinthiacus* Bernard 1957.

Leptothorax s. saxonicus n. sp. was studied on the basis of 180 workers and 80 queens originating from 65 samples taken in Saxonia, Bohemia, Moravia, Slovakia, Austria, Bulgaria and Serbia.

3 samples of *Leptothorax melas* Espadaler, Plateaux & Casevits-Weulersse, 1984 from Corsica were studied, which consisted of 11 workers and 1 queen. This material included 6 paratype workers and 1 paratype queen from Asco.

The N African species *L. normandi* Santschi, 1912 was studied on the basis of the type series consisting of 5 workers and 2 queens (Locus typicus: Le Kef/Tunisia).

4. *Leptothorax nyanderi* slavonicus nov. subsp.

4. 1. Type material

As holotype was designated a queen labelled »Kr. Görlitz, 19.3.1993, Schönau-Berzdorf, Hutberg, g31«. Paratypes 3 queens and 35 workers labelled »Kr. Görlitz, 19.3.1993, Schönau-Berzdorf, Hutberg«.

4. 2. Description

Queen (Figs. 15, 17, 20): head broad, occipital corners fully rounded, genae slightly converging frontad. Clypeus with 11 - 20 fine longitudinal microcarinae. Frons of head with very clear, linear, longitudinal microcarinae; a transversal line between the frontal carinae, set posterior of the frontal triangle, crosses 19 - 27 microcarinae; between the microcarinae with weak, irregular microsculpture. Pronotum, mesonotum and mesopleurae with a similar type of sculpture as on frontal head. Scutellum with longitudinal microrugae which are reduced in the median area. Propodeum with regular microrugae, their interspaces with more pronounced transversal or reticulate microsculpture. Propodeal slope with reticulate sculpture of which the transversal component is much more pronounced. Metapleurae with a longitudinal sculpture which is stronger than on propodeum. Propodeal spines strong and rather long, regularly showing a slight downward curvature (Fig. 15). In dorsal view the spine tips are less acute than in *nylanderi*. Petiole in lateral view relatively high, with a straight or slightly concave frontal profile; the dorsum with a small plateau and steep posterior slope. Sides of petiole with reticulate microsculpture the meshes of which have 12 - 13 µm diameter. Dorsum of petiole and postpetiole with reticulate microsculpture and a few longitudinal microrugae. The average pigmentation pattern is: Posterior half of tergites and sternites blackish brown. Anterior half of tergites, legs, scape, funiculus and mandibles yellowish. Dorsum of head and scutellum dark yellowish brown. Remaining body parts light to medium yellowish brown. Data of 212 queens (mean ± standard deviation, minimum-maximum): HL 739.3 ± 19.6 (665-803), HW 751.9 ± 19.6 (671-806), ML 1171.6 ± 35.8 (1034-1284), SPBA/ML 0.2864 ± 0.0128 (0.260-0.330), SPTI/ML 0.2902 ± 0.0134 (0.249-0.324), HL/HW 0.9835 ± 0.0182 (0.930-1.026), ISP 1.973 ± 0.138 (1.59-2.46), ML/HW 1.5584 ± 0.0337 (1.475-1.662), ML/HS 1.5714 ± 0.0288 (1.488-1.672), FR/HS 0.3748 ± 0.0079 (0.360-0.393), SL/HS 0.6966 ± 0.0174 (0.661-0.722), PE/HS 0.3027 ± 0.0171 (0.267-0.337), PP/HS 0.4245 ± 0.0222 (0.390-0.460).

Worker (Figs. 5, 6, 10): head broad and with rounded sides. Clypeus with 9 - 18 fine longitudinal microcarinae. Frons of head with very clear, linear, longitudinal microcarinae. A transversal line between the frontal carinae, set posterior of the frontal triangle, crosses 24 - 25 microcarinae. The interspaces between the microcarinae show few weak anastomoses or are feebly chagrinate. Mesosoma with longitudinal rugosity superimposing the reticulate microsculpture. The longitudinal component is frequently absent on the dorsal mesosoma. Mesopropodeal depression notable but not deep. Propodeal spines long and strong, normally showing a slight downward curvature. Outer distance of spine base and spine tips clearly larger than in *nylanderi*. Petiole and postpetiole covered by a reticulate microsculpture. Petiole in lateral view with slightly concave frontal profile, a rather truncated dorsum and a steep posterior slope. Overall pigmentation lighter and more yellowish than in *nylanderi*. Posterior half of tergites dark to blackish brown. Appendages, anterior half of tergites,

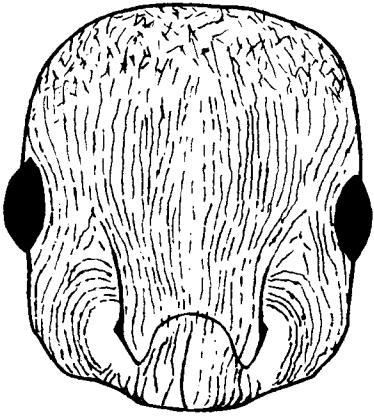


FIG. 7 SAXO

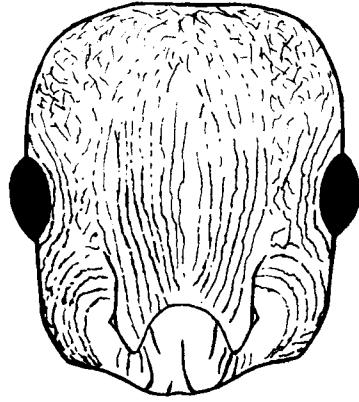


FIG. 8 SORD

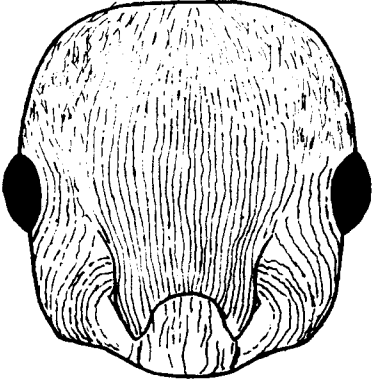


FIG. 9 NYLA

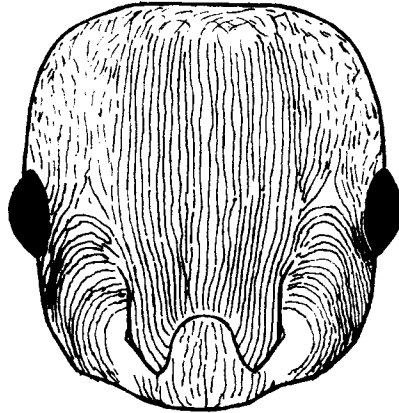


FIG. 10 SLAV



Figs. 7-8

Head capsule of workers of *Leptothorax s. saxonicus*, *s. sordidulus*, *n. nylanderi* and *n. slavonicus*. The scale bar represents 512 μ m.

mandibles, clypeus and genae yellowish. Dorsum of head light to medium yellowish brown. Mesosoma, petiole and postpetiole yellowish or yellowish with a brownish tinge. Data of 847 workers: HS 658.9 ± 32.4 (551-748), HL/HW 1.0524 ± 0.0191 (0.971-1.120), SL/HS 0.7512 ± 0.0135 (0.698-0.785), FR/HW 0.3754 ± 0.0109 (0.352-0.412), PE/HS 0.2649 ± 0.0131 (0.230-0.298), PP/HS 0.3714 ± 0.0157 (0.330-0.430), PP/PE 1.4482 ± 0.0409 (1.345-1.528), ISP 2.192 ± 0.171 (1.72-2.79), SPBA/HS 0.3025 ± 0.0178 (0.248-0.399), SPTI/HS 0.3763 ± 0.0196 (0.313-0.475).

4.3. Differential diagnosis and comments on similar species

The taxa *L. nylanderi*, *slavonicus* and *normandi* share certain characters that separate them from the taxa *melas*, *sordidulus*, *carinthiacus* and *saxonicus*. These are mainly the proportions of the head (nest means of worker HL/HW 1.028-1.103 in the first group and 1.112-1.222 in the second group) and the mesosoma proportions in the queens (ML/HS 1.51-1.69 in the first and 1.67-1.79 in the second group). The characters of the second group are discussed in more detail in section 5 while the first group is discussed here.

Leptothorax normandi from N Africa, of which the type series was studied, is different from both *nylanderi* and *n. slavonicus* in having a significantly narrower petiole in the worker. The ratio PE/HS is 0.240 ± 0.006 in *normandi*, 0.260 ± 0.010 in *nylanderi* and 0.265 ± 0.013 in *slavonicus*. Further, in the *normandi* worker, the longitudinal component of the dorsal head sculpture is less developed. In this character *normandi* resembles *saxonicus*.

A morphometric comparison of *nylanderi* and *slavonicus* is given in Tables 1, 2 and 3. In dorsal view the worker of *slavonicus* differs from *nylanderi* in particular by its larger SPBA and SPTI (Figs. 4, 6). In lateral view its spines frequently show a slight downward curvature which is missing in *nylanderi* (Fig. 3) and the ISP is on average larger. These separating characters occur also in the queens (Figs. 15 - 18). The best numeric characters to discriminate queens are SPBA/ML, SPTI/ML and ML/HS.

In order to obtain a better discriminative power of certain morphometric indices in workers, the variation produced by allometries was removed by calculating corrected values. The ratios SPBA/HS, SPTI/HS, which are most useful in discriminating *slavonicus* ssp. n. and *nylanderi*, increase with growing body size. This size-relation was described by linear regression functions for each taxon separately. With these functions then was calculated a cumulative standard regression giving the best fit to the empirical data of the two species. These standard regressions were

$$\text{SPBA/HS} = 0.00016104 \text{ HS} + 0.1804$$

$$\text{SPTI/HS} = 0.00016615 \text{ HS} + 0.2460.$$

The size-corrected indices SPBA_{cor} and SPTI_{cor} were then computed by division with the values of these standard regression functions. Values < 1 indicate a *nylanderi* character and such > 1 a *slavonicus* character.

Then a linear discriminant $D(2)$ was calculated as

$$D(2) = 0.49 \text{ SPBA}_{\text{cor}} + 0.51 \text{ SPTI}_{\text{cor}}$$

The nest sample means of $D(2)$, SPBA_{cor} , SPTI_{cor} and of other morphometric characters are shown in Table 1. Except of HS and HL/HW, the means of all characters shown in Table 1 are different for $p < 0.0001$. The worker of *slavonicus* has a clearly larger basal and apical distance of spines and a clearly larger spine index. The reduction of the head length ratio and of the head size in *slavonicus* is very weak but significant for $p < 0.0001$ if the t test is made on the basis of all 847 and 752 measured individuals of *slavonicus* and *nylanderi*.

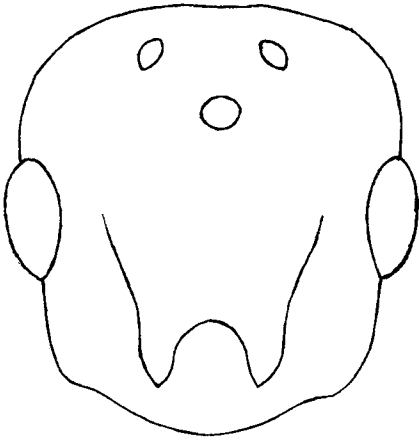


FIG. 11 SORD

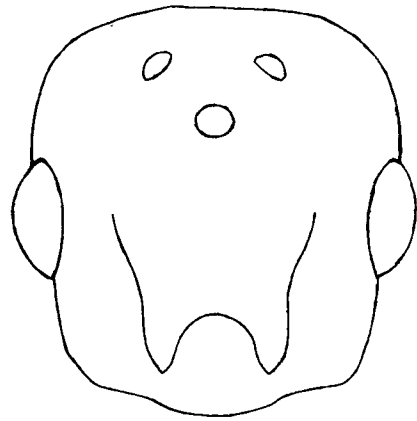


FIG. 12 SAXO

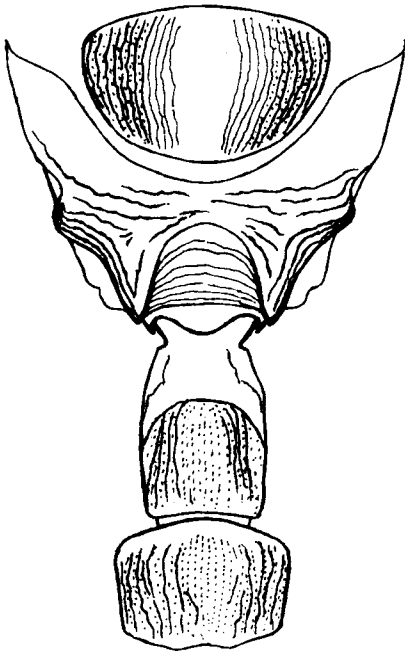


FIG. 13 SORD

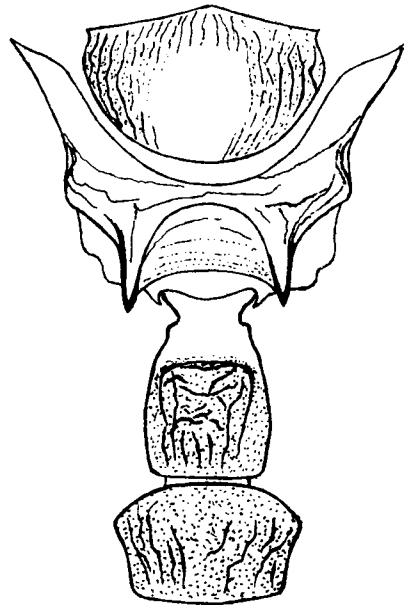


FIG. 14 SAXO

Figs. 11-14 Outlines of head capsule and dorsal view of posterior mesosoma, petiole and postpetiole of queens of *L. sordidulus* and *s. saxonicus*. The scale bar represents 512 μm .

Table 1 Distribution of nest sample means of 204 nests samples of *Leptothorax nylanderi nylanderi* and 231 nest samples of *L. nylanderi slavonicus*. Given are the arithmetic mean, standard deviation and extreme values of several morphometric data and of the discriminant D(2).

	slavonicus (n=231)			nylanderi (n=204)		
	mean	SD	range	mean	SD	range
D(2)	1.0634	0.0377	0.980-1.181	0.9384	0.0266	0.850-0.998
HS	660.1	24.6	569-711	664.4	21.4	596-711
HL/HW	1.0524	0.0147	1.005-1.103	1.0553	0.0124	1.030-1.087
ISP	2.2006	0.1285	1.862-2.527	1.8902	0.0912	1.737-2.063
SPBA/HS	0.3049	0.0133	0.274-0.344	0.2689	0.0101	0.238-0.293
SPTI/HS	0.3781	0.0149	0.342-0.416	0.3353	0.0112	0.296-0.363
SPBA _{cor}	1.0635	0.0433	0.966-1.209	0.9356	0.0337	0.833-1.017
SPTI _{cor}	1.0632	0.0408	0.956-1.169	0.9411	0.0298	0.839-1.017

A sufficiently good discrimination of the queens of *slavonicus* and *nylanderi* was possible on the individual level and without allometric corrections. A linear discriminant D(4) to separate the queens was calculated as

$$D(4) = 6.11 \text{ SPBA/ML} + 6.00 \text{ SPTI/ML} - 0.75 \text{ ML/HS} + 0.10 \text{ ISP.}$$

The discriminant D(4) and other morphometric data of individual queens of *slavonicus* and *nylanderi* are shown in Table 2. All means shown in the table are significantly different for $p < 0.0001$. The *slavonicus* population from the S Bulgarian mountains has smaller ISP (1.710 ± 0.080) and SPTI/ML (0.2633 ± 0.0077) as usual for this taxon and was not considered in Table 2. This decrease of ISP and the lowered distance of spine tips is also found in the workers from this region ($ISP 1.836 \pm 0.118$, $SPTI/HS 0.3441 \pm 0.0182$).

Table 2 Data of 141 queens of *Leptothorax nylanderi nylanderi* and of 212 queens of *L. nylanderi slavonicus*. Given are the arithmetic mean, standard deviation and extreme values of several morphometric data and of the discriminant D(4).

	slavonicus (n=212)			nylanderi (n=141)		
	mean	SD	range	mean	SD	range
D(4)	1.0577	0.0324	0.982-1.135	0.9404	0.0269	0.867-1.011
ML	1171.6	35.8	1034-1284	1193.1	43.9	1018-1274
SPBA/ML	0.2864	0.0128	0.260-0.330	0.2487	0.0098	0.216-0.270
SPTI/ML	0.2902	0.0134	0.249-0.324	0.2490	0.0098	0.230-0.274
ML/HS	1.5714	0.0288	1.488-1.672	1.6109	0.0300	1.519-1.689
ISP	1.9730	0.1381	1.59-2.46	1.7735	0.1506	1.40-2.23

4.4. The contact zone of *slavonicus* and *nylanderi* in Germany

Fig. 19 shows the distribution of *slavonicus* and *nylanderi* in the German countries Sachsen, Sachsen-Anhalt and Thüringen. In this region, the distributional border between both taxa is more or less parallel to the Elbe river. It goes from SE to NW in Sachsen and turns north in Sachsen-Anhalt. The distribution in Mecklenburg-Vorpommern and Niedersachsen is poorly studied. The few records of *nylanderi* from the western part of Mecklenburg-Vorpommern suggest that the distributional border could approximately run from Magdeburg north to Schwerin. The basic picture of distribution of *nylanderi/slavonicus* in Germany shows similarities to such avian examples as *Corvus coronel*/C. *cornix* and *Luscinia megarhynchos*/L. *luscinia* or to such as the house mouse siblings *Mus musculus*/domesticus. This suggests to common traits in the distributional history of all these taxa during the Pleistocene and the postglacial period.

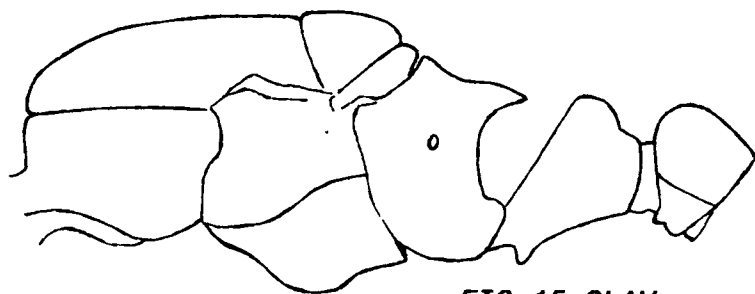


FIG. 15 SLAV

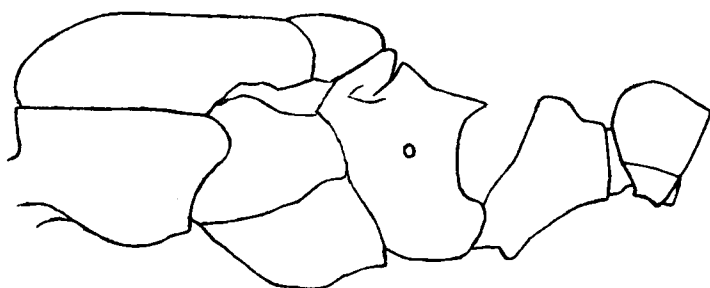


FIG. 16 NYLA

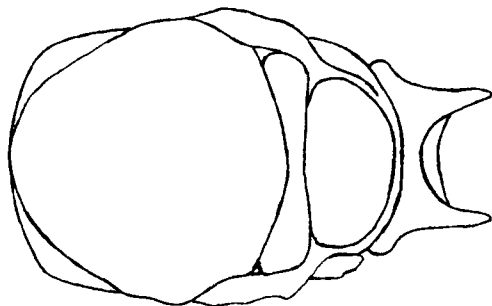
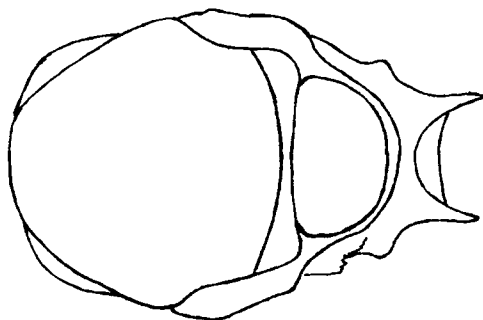


FIG. 17 SLAV

FIG. 18 NYLA



Figs. 15–18 Mesosoma, petiole and postpetiole in lateral view and mesosoma in dorsal view of queens of *L. n. slavonicus* and *n. nylanderi*. The scale bar represents 824 μm .

There is no obvious difference between *nylanderi* and *slavonicus* in habitat selection and apparently they form equivalent ecological niches. Both taxa are closely associated with the temperate deciduous woodland, in particular with the *Quercus*-mixed-forest. In Fennoscandia they do not occur in the subboreal *Pinus-Betula* woodland, and in Central Europe their vertical distribution ends in the lower submontane region. Refugia of deciduous trees are thought to have survived the last Pleistocene in SW Iberia, S Italy and the Balkans (HUNTLEY 1988). In cores from Central European peat bogs the first *Quercus* pollen was detectable in the Preboreal around 9500 BP and was found in a higher percentage around 8000 BP (SCHUBERT 1966, FIRBAS 1949-52). The *Quercus*-mixed-forest was established here as predominant woodland vegetation in the warm period of the Atlantic (7500 - 6000 BP). The spreading of a *Leptothorax* species capable of dispersal by active flight should be at least as rapid as the passive transport of *Quercus* acorns by vertebrates. Therefore, it is reasonable to assume that ants and *Quercus* vegetation almost simultaneously invaded new areas and it is very likely that both taxa met in Central Europe and East Germany not later than 7000 BP.

Are there morphological gradients within the populations of *nylanderi* and *slavonicus* along a transect from W to E or SW to NE and is there a substantially higher number of intermediates in the contact zone? An analysis of this question was performed in the following way. The distributional border depicted in Fig. 19 was used as reference line and each point of this line represents the transect-km 0. The position of each locality was then described by the shortest distance from the border line. Localities W or SW of the border line have negative km values. This figure is termed in the following as »transect-km«. The best chances to detect morphological gradients or putative hybrids are given when the most discriminative characters, in particular the discriminants D(2) and D(4) are considered. Fig. 20 and Tabs. 3 and 4 show the discriminant values of nest samples of workers and of individual queens as function of the transect-km.

Table 3 Discriminant values of 393 nest samples of workers of *Leptothorax nylanderi nylanderi* and *Leptothorax nylanderi slavonicus* along a cumulative W-E transect in Germany. The size of a nest sample varied between 3 and 7 workers. A total of 1600 workers was measured. The terminus »transect-km« must be interpreted as shortest distance to the distributional border of both taxa. The interval (-12, +13] marks the contact zone. D(2) was calculated from the two most discriminative ratios SPBA/HS and SPTI/HS with correction of allometric effects.

transect-km interval	discriminant D(2) <i>nylanderi</i>	discriminant D(2) <i>slavonicus</i>
(-533, -112]	0.9250 ± 0.0309, n=22	
(-112, -87]	0.9270 ± 0.0300, n=21	
(-87, -62]	0.9449 ± 0.0273, n=14	
(-62, -37]	0.9380 ± 0.0251, n=45	
(-37, -12]	0.9399 ± 0.0255, n=52	
(-12, 13]	0.9490 ± 0.0231, n=37	1.0642 ± 0.0373, n=73
(13, 38]		1.0642 ± 0.0402, n=71
(38, 63]		1.0664 ± 0.0427, n=19
(63, 88]		1.0710 ± 0.0285, n=16
(88, 113]		1.0588 ± 0.0264, n=11
(113, 138]		1.0533 ± 0.0274, n=12

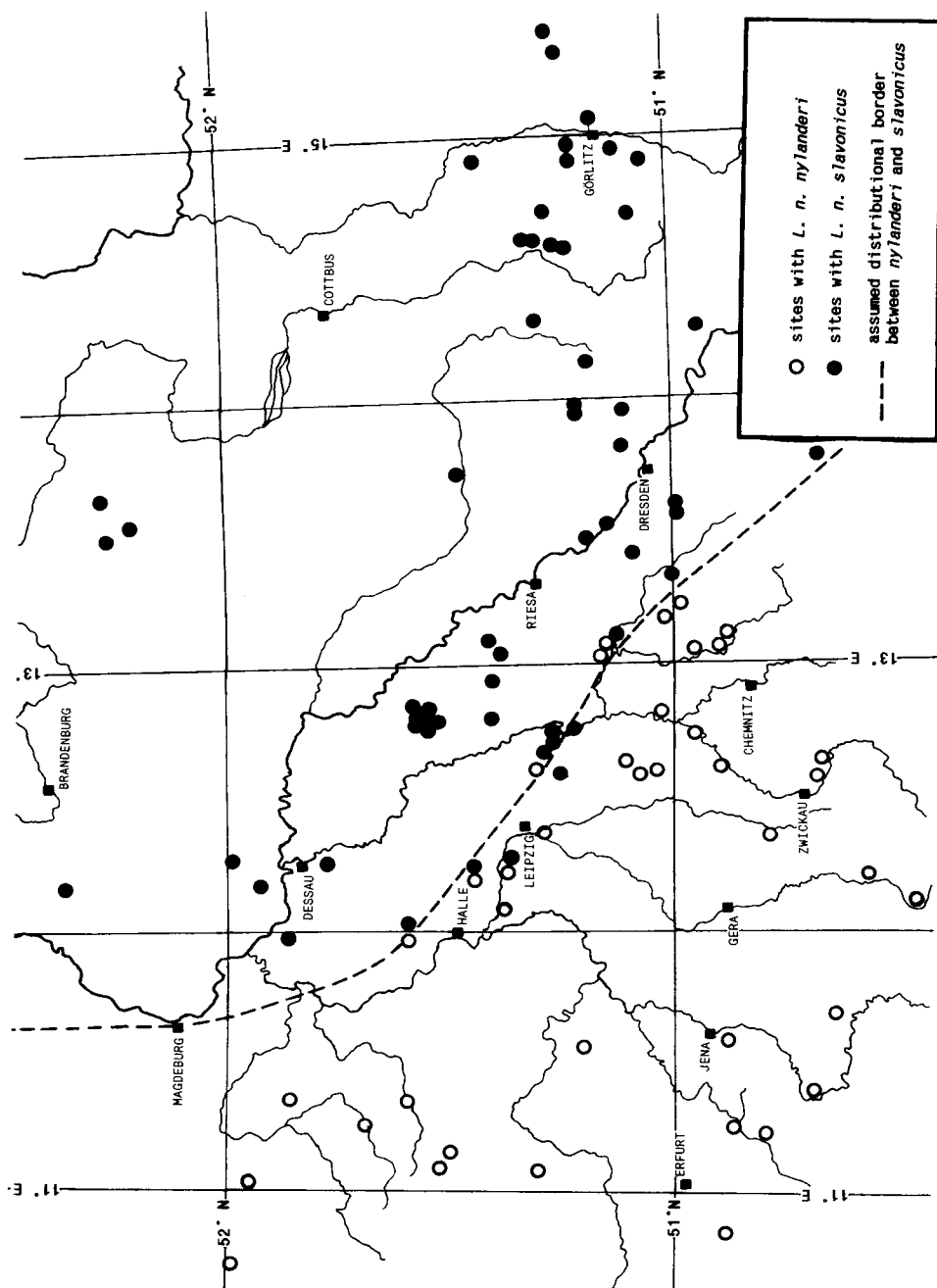


Fig. 19

Distribution of the subspecies *L. nylanderii slavonicus* and *L. n. nylanderii* in the German countries Sachsen, Sachsen-Anhalt and Thüringen. The dots represent sampling sites. The number of samples taken in a site varies from 1 to 20, but in most of the cases 3-7. Syntopic occurrence of both taxa could be found in only 4 sites situated very near to the distributional border.

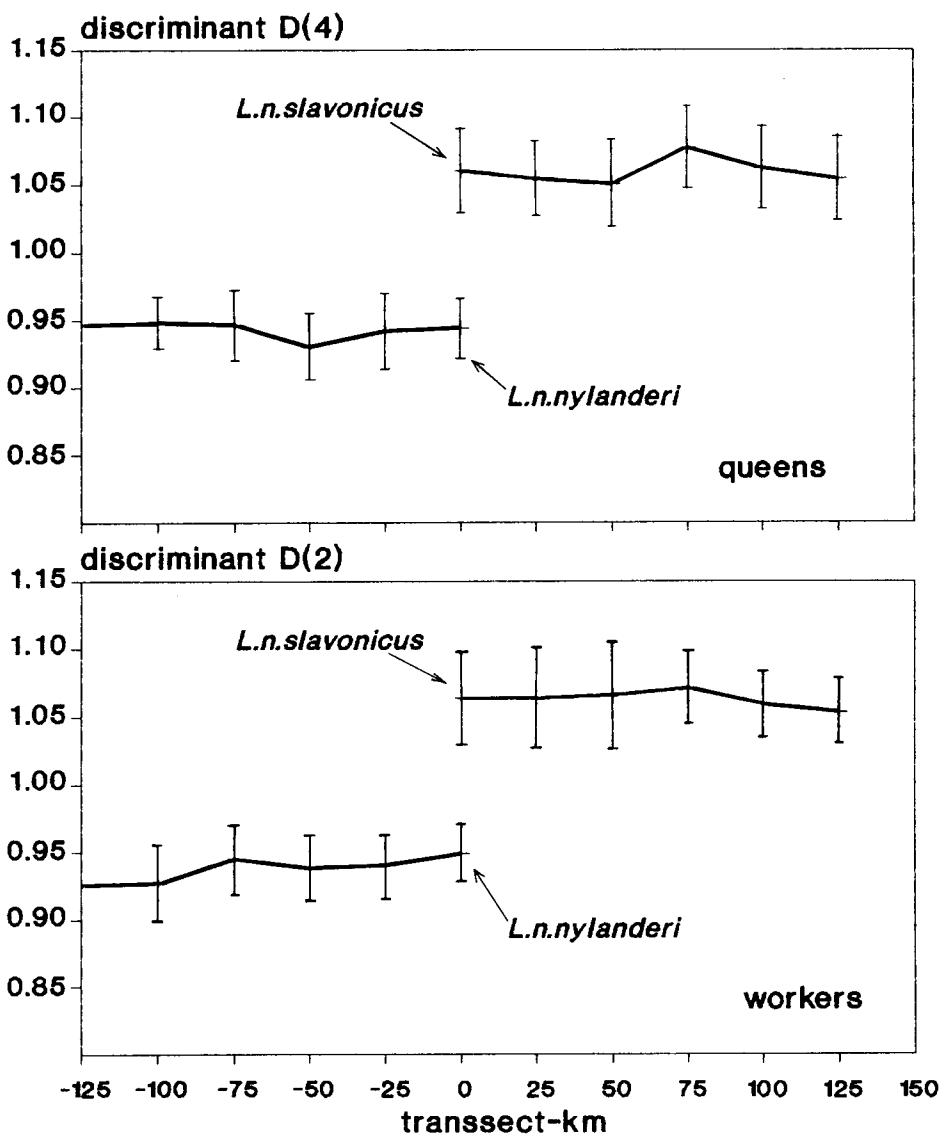


Fig. 20 Discriminant values D(2) and D(4) of workers and queens of *Leptothorax n. nylanderi* and *L. n. slavonicus* plotted against the shortest distance from the distributional border of both taxa. The km 0 represents the distributional border depicted in Fig. 19. Negative km values indicate positions W or SW from the distributional border.

Table 4 Discriminant values of 321 queens of *Leptothorax nylanderi nylanderi* and *Leptothorax nylanderi slavonicus* along a cumulative W-E transect in Germany. The terminus »transect-km« must be interpreted as shortest distance to the distributional border of both taxa. The interval (-12, +13] marks the contact zone. The discriminant D(4) was calculated from the 4 most discriminative ratios SPBA/ML, SPTI/ML, ML/HS and ISP.

transect-km interval	discriminant D(4) <i>nylanderi</i>	discriminant D(4) <i>slavonicus</i>
(-533, -112]	0.9358 ± 0.0265, n=12	
(-112, -87]	0.9478 ± 0.0203, n=22	
(-87, -62]	0.9466 ± 0.0284, n=13	
(-62, -37]	0.9296 ± 0.0266, n=29	
(-37, -12]	0.9422 ± 0.0301, n=35	
(-12, 13]	0.9439 ± 0.0236, n=26	1.0596 ± 0.0332, n=62
(13, 38]		1.0541 ± 0.0302, n=72
(38, 63]		1.0497 ± 0.0354, n=20
(63, 88]		1.0773 ± 0.0328, n=13
(88, 113]		1.0619 ± 0.0331, n=20
(113, 138]		1.0542 ± 0.0334, n=16

Despite of 7000 years possibility for hybridization in East Germany, the different morphological characters of both taxa apparently remained stable. There are no obvious morphological gradients towards the distributional border and no significantly increased numbers of intermediates in the contact zone that could indicate a genetic exchange. A linear regression analysis of the data presented in Tabs. 3 and 4 could not demonstrate any gradient within the queen samples of *nylanderi* and *slavonicus* and within the worker sample of *slavonicus*. However, a weak gradient could be demonstrated in the workers of *nylanderi*:

$$D(2) = 0.00007238 X + 0.9435 \quad (r=0.265, p < 0.0001)$$

with X being the transect-km value. This function calculates a D(2)=0.9290 for a site 200 km W of the distributional border and a D(2)=0.9435 for a site directly situated on the distributional border. This increase is only 13 % of the absolute difference of the *nylanderi* and *slavonicus* discriminant values in the 'hot' contact zone. The samples from Hessen, N Bayern, Nordrhein-Westfalen and Baden-Württemberg, having a mean distance of 300 km from the distributional border, have significantly smaller discriminants than those from the contact zone when tested in a χ^2 test ($p < 0.01$). This refers to both queens and workers.

There are only few nest samples in the contact zone which external morphology suggests to a hybrid identity. These intermediates have values of D(2) and D(4) in the interval (0.98, 1.01). If the populations within the contact zone are compared with those outside the contact zone in a χ^2 test, there is not detectable any significant increase of intermediates within the contact zone (Tab. 5). This refers to workers, queens and a cumulative consideration of both castes. The ratio of intermediates outside of the contact zone is 5,4 % and inside the contact zone 6,7 %. This gives no suggestion to hybridisation events.

Table 5 Frequency of unclear intermediate samples and of clear samples, i.e. those belonging either to the subspecies *nylanderi* or *slavonicus*, within the contact zone and outside. As intermediates were defined samples with values of the discriminants D(2) and D(4) in the interval (0.98, 1.01) and as clear subspecies were defined samples with discriminant values ≤ 0.98 or ≥ 1.01 .

	intermediates		clear subspezies	
	within contact zone km (-30, +30]	outside of contact zone	within contact zone km (-30, +30]	outside of contact zone
queens	8	10	168	154
workers	16	8	192	179
both	24	18	360	333

The findings presented above show that the external morphology can not give an indication for a substantial exchange of genes between *slavonicus* and *nylanderi*. The Figs. 19 and 20 show that the geographic replacement of *slavonicus* and *nylanderi* occurs abruptly and that there is obviously a very weak distributional overlap. This raises the question which kind of selection could have stabilized this parapatric situation. It occurs in a geographical region without natural barriers or abrupt changes in climate and vegetation. Selection resulting from different adaptations to *external* environment is therefore much less likely than a selection against hybrids operating in the epigenetic environment of alleles. It is unlikely to interpret this phenomenon as a clinal step within a tension zone of hybridizing taxa in the sense of BARTON & GALE (1993). If so, this clinal step should be extremely steep - i.e. should occur within a distance of only 1 - 3 km. This seems improbable for ants which can disperse by flight.

However, the PGI alloenzyme data obtained by Per Douwes (DOUWES pers. comm.) indicate that hybridisations are not so rare in the 'hot' contact zone (km -12 to km 13). The frequency of heterozygotes and of recombinant genotypes is significantly increased in the contact zone. Further, there is obviously a moderate introgression of PGI genes in both directions. Single PGI alleles of *slavonicus* are detectable 95 km west and such of *nylanderi* 35 km east of the distributional border.

The taxonomic treating of such examples is difficult. Entities that are subdivided (or joined) by hybrid zones cannot simply be categorized as either conspecific or as belonging to different species (HARRISON 1993). To describe *slavonicus* in this paper as a subspecies of *nylanderi* is thus a matter of personal taste - to describe it as a different parapatric species would be equally justified.

5. *Leptothorax sordidulus saxonicus* nov. subsp.

5.1. Type material

Holotype: a queen labelled »Sachsen: Kr. Löbau, Löbauer Berg, 1983. 07.27-473«. Paratypes 4 queens and 8 workers from the same nest sample as holotype. Depository: Staatliches Museum für Naturkunde Görlitz.

5.2 Description

Queen (Figs. 12, 14): head more elongated than in *nylanderi* and *slavonicus* but less than in *sordidulus*. Genae rather straight, slightly converging frontad. Clypeus with 10 - 14 weak longitudinal microrugae which may be reduced in the median area. Frons of head with longitudinal microrugae the interspaces of which are chagrinat. A transversal line between the frontal carinae, set posterior of the frontal triangle, crosses 18 - 25 microrugae. Mesosoma longer than in *nylanderi* and *slavonicus*. Pronotum, mesopleurae and lateral propodeum with longitudinal microrugosity which is weaker and less linear than in *nylanderi* and *slavonicus*. The interspaces between the rugae on lateral propodeum and metapleurae with reticulate microsculpture. Scutellum with longitudinal microrugosity which is reduced in the shining median area. Propodeal slope with transversal microrugosity. Propodeal spines rather short but normally slender and with acute tips (Fig. 14). In lateral view, the main orientation of spines is not strictly caudad as in *nylanderi* but shows a slight dorsad trend. Sides of petiole with reticulate microsculpture, the meshes of which have a diameter of 8 - 10 μ m. Petiole in lateral view with slightly concave frontal profile, a rather high node with a narrow, rounded top and a steep, slightly convex posterior slope. Postpetiole in dorsal view trapezoidal, with straight sides that notably converge caudad. Dorsum of postpetiole with irregular reticulate microsculpture and a few longitudinal rugae. Dorsum of petiole with few irregular rugae. Pigmentation on average darker than in *nylanderi* and *slavonicus*, having a more dirty brownish instead of a yellowish tinge. Dorsum of head, scutellum, dorsum of waist and mesopleurae dirty brown. Posterior half of tergites blackish brown. Anterior half of tergites light yellowish brown.

Data of 64 queens: HL 768.9 ± 23.0 (693-822), HW 742.8 ± 23.3 (698-802), ML 1300.8 ± 50.3 (1162-1393), SPBA/ML 0.2412 ± 0.0103 (0.216-0.262), SPTI/ML 0.2361 ± 0.0111 (0.206-0.264), HL/HW 1.0350 ± 0.0190 (0.990-1.074), ISP 1.637 ± 0.124 (1.42-1.93), ML/HW 1.7511 ± 0.0359 (1.660-1.839, ML/HS 1.7207 ± 0.0294 (1.668-1.790), FR/HS 0.3507 ± 0.0064 (0.339-0.360),

SL/HS 0.7160 ± 0.0125 (0.691-0.738), PE/HS 0.3082 ± 0.0150 (0.275-0.330), PP/HS 0.4207 ± 0.0197 (0.371-0.461).

Worker (Figs. 2, 7): Head in dorsal view more elongated than in *nylanderi* or *slavonicus*; genae more straight. Clypeus with 8 - 13 fine longitudinal microcarinae; a median and 2 paramedian microcarinae are frequently more pronounced. Compared to *nylanderi* and *slavonicus*, the longitudinal component of microsculpture on frons of head is much less pronounced and the reticulate, transverse component more expressed. A transversal line between the frontal carinae, set posterior of the frontal field, crosses 14 - 21 microcarinae. Mesosoma with reticulate microsculpture which is superimposed by longitudinal rugosity in particular on lateral mesosoma. Mesopropodeal impression in the majority of specimens well defined. Propodeal spines rather short but narrow-based and acute; in contrast to *nylanderi* and *slavonicus*, they are more erected, showing a dorsocaudal orientation. Postpetiole and petiole covered by a reticulate microsculpture. Postpetiole in dorsal view in most of the cases trapezoidal, with sides converging caudad. Overall pigmentation darker than in *nylanderi* but definitely lighter than in *sordidulus*. The average pigmentation pattern is: head dark to blackish brown; mandibles, antennae and legs yellowish brown; mesosoma, petiole and postpetiole yellowish brown to medium brown (in *sordidulus* blackish brown); tergites blackish brown, except for their anterior third which is of a lighter yellowish brown. Data of 69 workers: HS 627.3 ± 34.0 (502-699), HL/HW 1.1224 ± 0.0155 (1.088-1.166), SL/HS 0.7670 ± 0.0132 (0.743-0.800), FR/HW 0.3720 ± 0.0101 (0.351-0.396), PE/HS 0.2605 ± 0.0132 (0.234-0.305), PP/HS 0.3614 ± 0.0150 (0.334-0.377), ISP 1.621 ± 0.123 (1.40-1.94), SPBA/HS 0.2580 ± 0.0152 (0.223-0.301), SPTI/HS 0.320 ± 0.0211 (0.277-0.361).

5.3. Differential diagnosis and comments on similar species

L. sordidulus Müller, 1923 has been described on a single worker found at Roditti in the region of Trieste. This type specimen was not available for comparison. However, Müller's statements on colour, sculpture, propodeal spines, petiole profile and mesopropodeal suture provide a good indication which ant is meant. *Leptothorax* ants which fit Müller's description are very abundant in the region of NE Italy and adjacent areas (A. SCHULZ and P. DOUWES, personal communication) and there is a low risk that the ants described here as *sordidulus* do not belong to the same species as Müller's specimen.

There is no doubt that *Leptothorax carinthiacus* Bernard, 1957 is a synonym of *sordidulus*. The type series of *carinthiacus*, taken at Viktring near Klagenfurt, only 110 km NNE of Trieste, is morphologically indistinguishable from the *sordidulus* series of NE Italy.

There are large similarities in sculpture, pigmentation, proportions and shape of body between *L. sordidulus* and *L. melas* Espadaler, Plateaux & Casevits-Weulersse, 1984. A separate identity of *melas* is indicated by its significantly longer head, longer scape and weaker mesopropodeal suture. Further, in *melas* the frontal and dorsal profile lines of the petiole meet in a sharp angle. Such a character combination is not seen in the *sordidulus* nest samples examined. The ratio HL/HW ranged from 1.179 to 1.242 in 11 worker specimens of *melas* which is outside the range known for *sordidulus* (1.099-1.174). The strongly elongated head of *melas* is also found in the investigated type queen and is indicated by the data given by ESPADALER, PLATEAUX & CASEVITZ-WEULERSSE (1984) for 20 type workers.

The best morphometric differentiation of *sordidulus* and *saxonicus* is found in the queens. *L. sordidulus* and *saxonicus* differ for the highest significance level ($p < 0.0001$) in HL/HW, ISP, SPTI/ML and ML/HW. A separation of 95 % of the queens is provided by a linear discriminant function with

$$D(4) = 7.60 \text{ SPTI/ML} - 0.58 \text{ HL/HW} + 0.625 \text{ ISP} - 0.526 \text{ ML/HW}$$

The data of $D(4)$ and of several morphometric characters are given in Tab. 6.

Table 6 Data of 64 queens of *Leptothorax sordidulus saxonicus* and of 20 queens of *L. sordidulus sordidulus*. Given are the arithmetic mean, standard deviation and extreme values of several morphometric data and of the discriminant D(4).

	saxonicus (n=64)			sordidulus (n=20)		
	mean	SD	range	mean	SD	range
D(4)	1.2958	0.1426	1.046-1.656	0.8119	0.1187	0.644-1.066
ML	1300.8	50.3	1162-1393	1358.6	34.0	1269-1420
SPBA/ML	0.2412	0.0103	0.216-0.262	0.2341	0.0089	0.216-0.250
SPTI/ML	0.2361	0.0111	0.206-0.264	0.1981	0.0119	0.178-0.219
ML/HS	1.7207	0.0294	1.668-1.790	1.7686	0.0297	1.713-1.828
ML/HW	1.7511	0.0359	1.660-1.839	1.8191	0.0364	1.767-1.904
ISP	1.637	0.124	1.42-1.93	1.402	0.123	1.24-1.67

Figs. 13 and 14 show the average differences of both taxa in the shape and surface structures of propodeum, petiole and postpetiole. The queen of *saxonicus* shows in dorsal view more pointed, spines with a narrow base, more distant spine tips and a more trapezoidal postpetiole. Further, the sculpture on the propodeum, on the propodeal slope and in the spine region is clearly less pronounced compared to *sordidulus*. The darker overall pigmentation of *sordidulus* is normally a good discriminating character. In *sordidulus* the antennal club is darker than the other funicular segments while in *saxonicus* the whole funiculus is equally pigmented in a light yellowish brown.

A perfect morphometric separation of *sordidulus* and *saxonicus* workers is not possible. Characters with highly significant differences are HL/HW and SPTI/SPBA (both $p < 0.0001$) as well as HS ($p < 0.001$) and PP/HS ($p < 0.002$). The overlap, however, of these characters is large even if considering nest sample means and no powerful discriminant function was found. So the most obvious separating character is the lighter coloration of the *saxonicus* worker, in particular on mesosoma. This character seems to be more or less stable throughout the range in Sachsen, Bohemia, Moravia, Slovakia, E Austria and Bulgaria. However, one worker nest series from a locality deeply within the range of *saxonicus* (Central Slovakia, SPR Boky, leg. P. Werner, 1987.07.20) shows a coloration as found in the *sordidulus* specimens from NE Italy and W Austria. The workers of *saxonicus* give the impression that the reticulate microsculpture on the petiole sides is weaker. This refers not to the diameter of the meshes, which is in both taxa 10 - 12 μm , but *saxonicus* seems to have weaker relief differences.

It is difficult to decide whether the new taxon *saxonicus* must be considered as good parapatric species or as subspecies of *sordidulus*. The differences in the morphology of the queens quote for a parapatric species pair but the situation in the workers is more compatible with the view that *saxonicus* is nothing but a distinct eastern subpopulation of *sordidulus*. The distinctness of the populations was most probably generated by a splitting up during the Pleistocene. One population surely survived in a S Appennine refuge area (*sordidulus*) and the other in a S Balkan refuge area (*saxonicus*). To which degree both taxa exchange genetic material in their present contact zone is unknown. This question can possibly be answered after an examination of much more samples from E Austria (Kärnten, Steiermark), Slovenia and the eastern border of Serbia. The treatment of *saxonicus* as subspecies as done here is provisional.

Finally, a comment must be given to *Leptothorax* samples collected by A. Schulz in the Grand Canyon du Verdon/Provence and in NE Turkey. These are very similar to *sordidulus* in overall morphology but differ considerably in at least one character.

The 3 nest samples with 9 workers from the Provence have a pigmentation pattern similar to *saxonicus* but show a ratio of FR/HW of 0.3535 ± 0.0040 . The one queen studied shows a ratio of FR/HS of 0.321. Consequently, the frontal carinae are in both castes much more approximated than in *sordidulus*, *saxonicus*, *nylanderi*, *slavonicus* and *normandi* (compare with Tab. 7, Tab. 8). This is a rather outstanding character.

The 7 nest samples with 25 workers from NE Turkey are by morphometry and pigmentation most similar to *sordidulus* but show a ratio of PE/HS of 0.2738 ± 0.0095 . The same ratio was 0.334 in the one queen studied. These data are much larger than in *sordidulus*. The taxonomic treatment of both the populations from the Provence and NE Turkey is unclear and needs further investigation.

Table 7 Morphometric data of individual *Leptothorax* workers; arithmetic means in heavy type, standard deviations in normal type

	HS	HL/HW	SL/HS	FR/HW	PE/HS	PP/HS	ISP	SPBA/HS	SPTI/HS
<i>nylanderi</i>	664.3	1.0556	0.7533	0.3744	0.2596	0.3776	1.894	0.2704	0.3363
(n=752)	30.2	0.0175	0.0167	0.0087	0.0104	0.0137	0.130	0.0147	0.0165
<i>slavonicus</i>	658.9	1.0524	0.7512	0.3754	0.2649	0.3714	2.192	0.3025	0.3763
(n=847)	32.4	0.0191	0.0135	0.0109	0.0131	0.0157	0.171	0.0178	0.0196
<i>normandi</i>	650.6	1.0780	0.7600	0.381	0.240	0.356	1.755	0.268	0.326
(n=5)	24.2	0.0154	0.0112	0.0093	0.0059	0.0040	0.249	0.0123	0.0140
<i>saxonicus</i>	627.3	1.1224	0.7670	0.3720	0.2605	0.3614	1.621	0.2580	0.3200
(n=69)	34.0	0.0155	0.0132	0.0101	0.0132	0.0150	0.123	0.0152	0.0211
<i>sordidulus</i>	601.4	1.1404	0.7626	0.3737	0.2541	0.3504	1.541	0.2626	0.3022
(n=37)	36.2	0.0174	0.0137	0.0160	0.0124	0.0189	0.156	0.0167	0.0263
<i>melas</i>	648.6	1.2074	0.7832	0.3627	0.2571	0.3602	1.526	0.2762	0.3263
(n=11)	24.7	0.0179	0.0110	0.0066	0.0107	0.0188	0.099	0.0166	0.0090

Table 8 Morphometric data of individual queens of *Leptothorax*; arithmetic means in heavy type, standard deviations in normal type

	HL	HL/HW	ML	FR/HS	SL/HS	ML/HS	SPBA/ML	SPTI/ML	ISP	PE/HS	PP/HS
<i>nylanderi</i>	734.5	0.9836	1193.1	0.3685	0.6954	1.6109	0.2487	0.2490	1.774	0.3059	0.4306
(n=141)	23.3	0.0185	43.9	0.0119	0.0114	0.0300	0.0098	0.0098	0.151	0.0137	0.0124
<i>slavonicus</i>	739.3	0.9835	1171.6	0.3748	0.6966	1.5714	0.2864	0.2902	1.973	0.3027	0.4245
(n=212)	19.6	0.0182	35.8	0.0079	0.0174	0.0288	0.0128	0.0134	0.138	0.0171	0.0222
<i>normandi</i>	789.5	1.0111	1258.5	0.3738	0.6465	1.6028	0.2665	0.2705	1.535	0.2954	0.3780
(n=2)	6.5	0.0124	9.5	0.0047	0.0112	0.0109	0.0095	0.0039	0.085	0.0034	0.0149
<i>saxonicus</i>	768.9	1.0350	1300.8	0.3517	0.7137	1.7207	0.2412	0.2361	1.637	0.3082	0.4207
(n=64)	23.0	0.0190	50.3	0.0060	0.0117	0.0294	0.0103	0.0111	0.124	0.0150	0.0197
<i>sordidulus</i>	789.4	1.0570	1358.6	0.3611	0.7230	1.7686	0.2341	0.1981	1.402	0.3005	0.4121
(n=20)	14.5	0.0173	34.0	0.0094	0.0152	0.0297	0.0089	0.0119	0.123	0.0093	0.0222
<i>melas</i>	780	1.117	1283	0.345	0.767	1.7361	0.251	0.235	1.47	0.319	0.445
(n=1)											

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